

Gulf and Caribbean Research

Volume 13 | Issue 1

January 2001

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DOI: 10.18785/gcr.1301.01

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Recommended Citation

Strasser, K. and D. Felder. 2001. Effects of Salinity on Development in the Ghost Shrimp *Callichirus islagrande* and Two Populations of *C. major* (Crustacea: Decapoda: Thalassinidea). *Gulf and Caribbean Research* 13 (1): 1-10.

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EFFECTS OF SALINITY ON DEVELOPMENT IN THE GHOST SHRIMP *CALLICHIRUS ISLAGRANDE* AND TWO POPULATIONS OF *C. MAJOR* (CRUSTACEA: DECAPODA: THALASSINIDEA)

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ABSTRACT Salinity (S) was abruptly decreased from 35‰ to 25‰ at either the 4th zoeal (ZIV) or decapodid stage (D) in *Callinectes sapidus* (Schmitt) and 2 populations of *C. major* (Say). Other larvae were maintained at stable 35‰ or 25‰ S throughout development. In *C. islagrande*, duration of ZIV did not vary among the stable salinities. However, a decrease of salinity at ZIV reduced the duration of this stage, suggesting that the S decrease could be a possible cue for acceleration of larval development. In the Gulf population of *C. major* duration of ZIV was significantly longer at stable 35‰ S than at stable 25‰ S; the latter equaled duration for larvae transferred from 35 to 25‰ S at ZIV. Development in the Florida Atlantic population of *C. major* was variable but similar at stable 35 and 25‰ S. In 2 of 3 such comparisons, larvae reared at a stable 35‰ S more often molted to a 5th zoeal stage and became deformed at D than those reared at a stable 25‰ S. *Callinectes sapidus* and the Gulf population of *C. major*, both of which inhabit lower salinity waters on the Louisiana coast, were more similar in larval responses to salinity than were the 2 populations of *C. major*. Adult habitat was a better indicator of larval response to salinity than was phylogenetic proximity.

INTRODUCTION

In decapod larvae, salinity (S) may impact rate of development (Vinuesa et al. 1985, Sulkin and Van Heukelem 1986, Gonçalves et al. 1995), size (Johns 1981), and behavior (O'Connor and Epifanio 1985, Tankersley et al. 1995). Previous studies examined the effect of decreased S on decapodids to determine if such a change serves as a cue for settlement (O'Connor and Epifanio 1985, Anger 1991, Forward et al. 1994, Wolcott and Devries 1994). A decrease in S may be important to species that pass through zoeal stages offshore and subsequently settle as decapodids (=megalopae) in estuaries. In *Uca pugnax* (Smith), duration of the decapodid stage was significantly shorter at 20‰ S than at 30‰ S (O'Connor and Epifanio 1985). While a decrease in S from 35 to 26‰ was not found to decrease significantly the duration of the decapodid stage of *Callinectes sapidus* (Rathbun) (Wolcott and Devries 1994), a decrease from 35 to 18‰ S significantly accelerated molting (Forward et al. 1994). Larvae of *Eriocheir sinensis* H. Milne-Edwards reared at 32‰ S accelerated molting when moved to 20‰ S at the decapodid stage (Anger 1991). However, maintaining decapodids at 32‰ S or moving them from 32 to 10‰ S increased the duration of the decapodid stage.

Several studies have also examined the effect of S on the zoeal phase of development. Success of larval development in *Armases cinereum* (Bosc) depends on an

estuarine-adapted 4th zoeal stage (Costlow et al. 1960); while the decapodid withstands a range of salinities, survival of the 4th zoeal stage is restricted to estuarine salinities. Slight to moderate decreases in S can accelerate the rate of zoeal development as in *Lithodes antarcticus* Jacquinot (Vinuesa et al. 1985) and *Armases miersii* (Rathbun) (Schuh and Diesel 1995); retard development as in *Armases cinereum* (Bosc) (Costlow et al. 1960), *Panopeus herbstii* Milne-Edwards (Costlow et al. 1962), *Menippe mercenaria* (Say) (Ong and Costlow 1970), *Palaemonetes vulgaris* (Say) (Sandifer 1973), *Uca pugnax* (Smith) (O'Connor and Epifanio 1985), *Armases angustipes* (Dana) (Anger et al. 1990), *Eriocheir sinensis* H. Milne-Edwards (Anger 1991), and *Carcinus maenas* L. (Anger et al. 1998); or have no obvious effect as in *Palaemonetes vulgaris* (Say) (Knowlton 1965), *Cancer irroratus* Say (Johns 1981), *Necora puber* (L.) (Mene et al. 1991), and *Menippe mercenaria* (Say) (Brown et al. 1992). In some species, development is shortest at intermediate salinities tested and somewhat retarded at extremes as in *Rhithropanopeus harrisi* (Gould) (Costlow et al. 1966, Gonçalves et al. 1995), and *Cardisoma guanhumi* Latreille (Costlow and Bookhout 1968). In *Macrobrachium nipponense* (De Haan) response of larvae to decreased S was shown to vary between populations (Ogasawara et al. 1979). However, most studies to date have examined the effect of S by maintaining larvae at a constant S throughout development.

In the genus *Callichirus*, larvae typically pass through 4 or 5 pelagic zoeal stages (ZI to ZV) before molting to the decapodid stage (D) (Strasser and Felder 1999a). Although D is usually thought to be receptive to settlement stimuli, previous studies have shown that settlement and development of *Callichirus major* (Say) are affected by cues received at the 4th zoeal stage (ZIV). The Gulf of Mexico and Florida Atlantic populations of *C. major* have been shown to be genetically distinct (Staton and Felder 1995), have different intertidal distributions (Felder and Griffis 1994), have morphological differences in their larvae (Strasser and Felder 1999a), and respond differently to settlement stimuli (Strasser and Felder 1999b). While ZIV plays an important role in settlement of both populations of *C. major*, this stage of *C. islagrande* (Schmitt) does not appear to respond to sand and adult-conditioned water (Strasser and Felder 1998, 1999b). The Florida Atlantic population of *C. major* inhabits waters of relatively constant 35‰ S. In contrast, the Gulf of Mexico endemic *C. islagrande* and the Gulf of Mexico population of *C. major* experience lower salinities which may range from 12-30‰ (Felder and Griffis 1994).

The present study was conducted to determine the effect of low (25‰) and high (35‰) salinities on numbers of instars and rates of development. The study included comparisons of decreased S effects during ZIV and D to determine whether S differentially accelerated molting.

MATERIALS AND METHODS

Experimental Protocol

Ovigerous females were collected by previously described methods (Felder 1978) from the bayward side of a barrier island (Isles Dernieres, LA; 29°03.8'N; 90°39.5'W) in March, April, August, and September 1997 for *C. islagrande* and the Gulf of Mexico popula-

tion of *C. major*, and from a sand flat on the north side of Sebastian Inlet (Florida; 27°51.7'N; 80°26.8'W) in May, June, and July, 1997 for the Florida Atlantic population of *C. major*. Ovigerous females were maintained in 20-cm diameter finger bowls with daily water changes until eggs hatched. Animals from the Gulf of Mexico were kept at 25‰ S, while those from the Florida Atlantic population of *C. major* were maintained at 35‰ S to approximate the S experienced in the natural habitat. Seawater was taken from well offshore Louisiana and Florida, filtered through a 30- μ m mesh, and aerated before use. Seawater at 25‰ S was made by diluting 35‰ S seawater with deionized water.

Upon hatching, ZI larvae were moved to individual compartments of a plastic tray and maintained at 27°C, on a 12 h light:12 h dark cycle, in filtered seawater of 35 or 25‰ S. Larvae (ZI to ZV) and decapodids were reared under 1 of 4 S protocols: a) 35‰ S throughout development to the first juvenile stage (J1), b) 35‰ S and moved to 25‰ S after the molt to ZIV, c) 35‰ S and moved to 25‰ S after the molt to D, d) 25‰ S throughout development to J1 (Figure 1). Once each day, animals were examined visually to assess their stage of development, moved to containers with new seawater, and fed freshly hatched *Artemia* nauplii (Great Salt Lake). For larvae placed in seawater that differed from S at hatching, the S was increased or decreased slowly 3 to 4 h before the experiment was initiated. In treatments with a decrease in S at ZIV or D (b and c), larvae were moved directly from 35 to 25‰ S and thus experienced an immediate shift in S. Each experiment began with 40 ZI larvae per treatment and all larvae remained isolated for the duration of the experiment. Each experiment, performed with larvae from the clutch of a single female, was repeated for a total of 2 clutches with both *C. islagrande* and the Gulf of Mexico population of *C. major* and 3 clutches with the Florida Atlantic population of *C. major*.

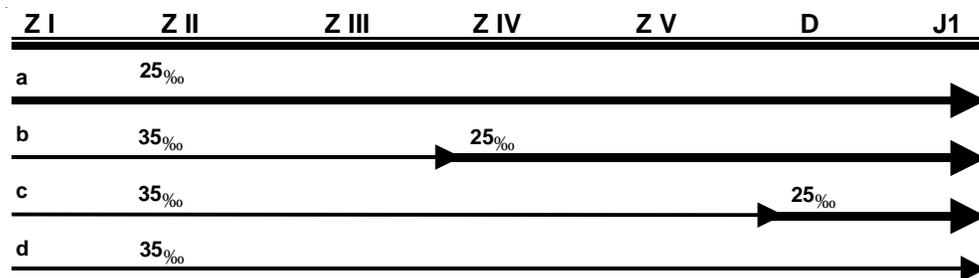


Figure 1 Experimental treatments: a) 25‰ S throughout development to J1; b) 35‰ S from ZI to ZIII and moved to 25‰ S after the molt to ZIV; c) 35‰ S from ZI to ZIV and moved to 25‰ S after the molt to D; d) 35‰ S throughout development to J1. Thin line designates stages maintained at 35‰ S and a thick line designates stages maintained at 25‰ S.

Analysis of data

To determine if a decrease in S at ZIV or D accelerated development, the durations of these stages (in days) were compared between treatments with a 1-factor ANOVA (type III sum of squares). The Tukey-Kramer post hoc test was used to test for significance among treatments. Only animals that survived to J1 were used in comparisons of stage durations. Within each species (or population of *C. major*) durations of ZI, ZII, and ZIII were compared between animals maintained at 25‰ S (treatment a) and 35‰ S (treatments b, c, and d combined) with t-tests. The proportion of larvae that passed through a 5th zoeal stage (ZV) and the proportion of deformed decapodids were also compared between treatments with Fisher’s exact-test. The term significant for all analyses is only used to describe differences in data sets that yield p-values < 0.05 with the statistical tests mentioned above. A resulting p-value ≥ 0.05 was considered to indicate that data sets did not differ significantly. Data were analyzed with Excel 5.0®, Super ANOVA 1.11®, and NCSS 6.0®.

RESULTS

Rate of development

In *C. islagrande* and the Gulf population of *C. major*, durations of ZI, ZII and ZIII were typically longer in animals maintained at 35‰ S at these stages (treatments b, c, and d) than in animals maintained at 25‰ S (treatment a) (Table 1). In the Florida Atlantic population of *C. major*, durations of ZI and ZII were similar

between animals maintained at both salinities; however, duration of ZIII was longer in animals maintained at 35‰ S than in animals maintained at 25‰ S, but this difference was significant only in Experiment 2.

The effect of S treatment on the duration of ZIV varied between species (Figure 2), but was found to be significant in experiments with both *C. islagrande* (1-factor ANOVA: Experiment 1, $F_{2,101} = 12.53$; $P = 0.0001$; Experiment 2, $F_{2,106} = 3.556$; $P = 0.032$) and the Gulf of Mexico population of *C. major* (1-factor ANOVA: Experiment 1, $F_{2,144} = 13.04$; $P = 0.0001$; Experiment 2, $F_{2,148} = 5.648$; $P = 0.0043$). However, there were differences between these species in the response of larvae to specific treatments. In *C. islagrande*, duration of ZIV was similar in animals maintained at a constant S from ZI to ZIV (either 25‰ S in treatment a, or 35‰ S in treatments c and d), but was much shorter in duration in larvae that experienced a decrease in S at this stage (treatment b).

Lower S also resulted in a shorter duration of ZIV in the Gulf of Mexico population of *C. major*. In both experiments with larvae of this population, the duration of ZIV was significantly shorter (Tukey-Kramer post hoc test, $P < 0.05$) in animals maintained at a constant 25‰ S (treatment a) or moved to 25‰ S at ZIV (treatment b) than in larvae maintained at 35‰ S through ZIV (treatments c and d) (Figure 2). This differed from results with the Florida Atlantic population of *C. major* (Figure 2), wherein treatment did not have a significant effect on the duration of ZIV in Experiments 1 and 2 but was marginally significant in Experiment 3. However in

TABLE 1

Mean duration in days (± SE) of ZI to ZIII for populations of *Callichirus* spp. maintained at 25‰ S (treatment a) or 35‰ S (treatments b, c, and d) from ZI to ZIII. Numbered experiments are for separate larval clutches. * = $P < 0.001$; ** = $P < 0.05$; with Student’s t-test.

Experiment	Number that reached J1		Mean duration ZI (SE)		Mean duration ZII (SE)		Mean duration ZIII (SE)	
	25‰	35‰	25‰	35‰	25‰	35‰	25‰	35‰
<i>Callichirus islagrande</i>								
1	31	74	2.00 (0.00)	2.03 (0.02)	*2.03 (0.03)	2.64 (0.07)	*2.55 (0.09)	3.07 (0.06)
2	35	80	*2.37 (0.08)	2.76 (0.06)	2.06 (0.04)	2.19 (0.04)	2.37 (0.08)	2.51 (0.06)
<i>C. major</i> (Gulf of Mexico)								
1	39	109	**1.95 (0.04)	2.05 (0.02)	*1.64 (0.08)	2.00 (0.03)	**2.03 (0.06)	2.24 (0.05)
2	34	117	*2.59 (0.09)	2.99 (0.09)	1.94 (0.10)	1.88 (0.03)	**1.94 (0.07)	2.13 (0.03)
<i>C. major</i> (Florida Atlantic)								
1	38	114	2.03 (0.03)	2.02 (0.01)	2.00 (0.0)	2.01 (0.01)	2.03 (0.03)	2.08 (0.02)
2	38	85	2.00 (0.00)	2.01 (0.01)	2.00 (0.0)	1.98 (0.02)	**1.97 (0.05)	2.12 (0.04)
3	38	93	1.45 (0.08)	1.59 (0.05)	1.76 (0.07)	1.77 (0.05)	2.00 (0.00)	2.11 (0.04)

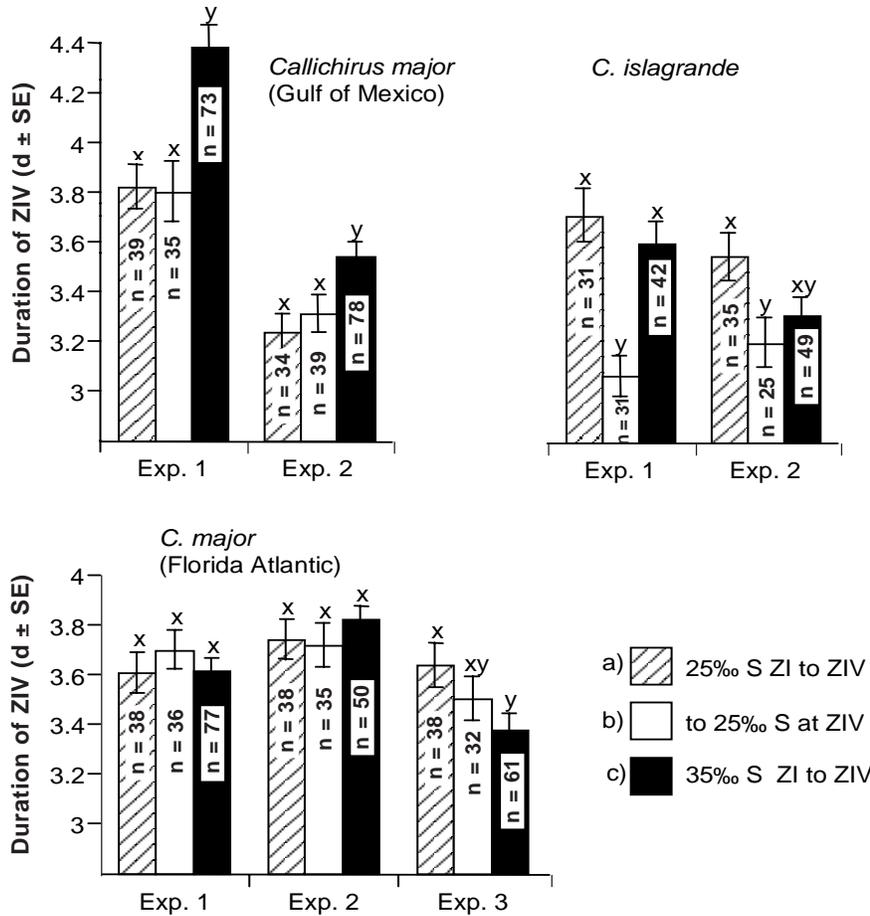


Figure 2. Mean duration in days \pm SE of ZIV when larval stages were alternatively reared at 25‰ S from ZI to ZIV (treatment a), 35‰ S from ZI to ZIII but moved to 25‰ S after the molt to ZIV (treatment b), or 35‰ S from ZI to ZIV (treatment d), lettered treatments corresponding to those in Figure 1. Number of animals that reached J1 in experimental treatment is given within each bar. Means with different letters above the error bar differ significantly ($P = 0.05$) within the given experiment for that population with the Tukey-Kramer post hoc test.

this case, duration of ZIV was found to be significantly longer in animals maintained at 25‰ S (treatment a) than in those maintained at 35‰ S from ZI to ZIV (treatments c and d) (Tukey-Kramer post hoc test, $P < 0.05$).

Unlike the 4th zoeal stage, the decapodid stage was not affected by a S change in either *C. islagrande* or the Gulf of Mexico population of *C. major* (Figure 3). The duration of the decapodid stage also did not change significantly in Experiments 1 and 3 with the Florida Atlantic population of *C. major*, but treatment did have a significant effect in Experiment 2 (1-factor ANOVA, $F_{3,119} = 9.502$; $P = 0.0001$). In Experiment 2, the duration of D was significantly shorter in animals maintained at 25‰ S (treatment a), or moved from 35 to 25‰ S at ZIV (treatment b), than in animals moved from 35 to 25‰ S at D (treatment c), or maintained at 35‰ S (treatment d), with the Tukey-Kramer post hoc test ($P < 0.05$).

Presence of a 5th zoeal stage

All of the larvae from the Gulf of Mexico population of *C. major* molted directly from ZIV to D (no ZV). While larvae in Experiment 1 with the Florida Atlantic population of *C. major* also followed this pattern, larvae from Experiments 2 and 3 often passed through a fifth zoeal stage (Table 2). In Experiment 2, the percentage of larvae that molted from ZIV to D (no ZV) was significantly higher in animals maintained at 25‰ S (treatment a, 100%) than in the other 3 treatments (b, 67%; c, 20%; d, 35%) according to results of Fisher's exact-test. Cultures with a decrease in S at ZIV (treatment b, 67%) had a significantly higher percentage of animals bypassing ZV, than did those maintained at 35‰ S through ZIV (treatments c, 20%; and d, 35%). In Experiment 3, significantly more larvae molted directly from ZIV to D in animals maintained at 25‰ S (treatment a, 90%) than among the other 3 treatments (b, 54%; c, 36%; d, 42%). Passing through a 5th zoeal stage reduced survival. Most

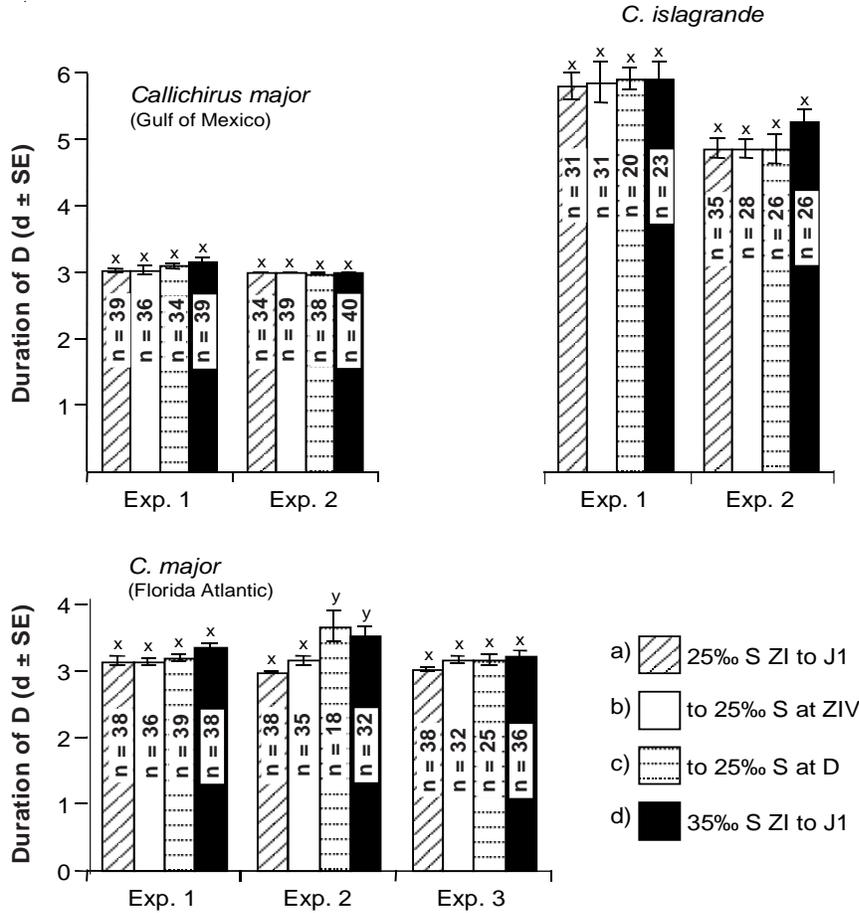


Figure 3. Mean duration in days \pm SE of D when larval stages were alternatively reared at 25‰ S from ZI to J1 (treatment a), 35‰ S from ZI to ZIII but moved to 25‰ S after the molt to ZIV (treatment b), 35‰ S from ZI to ZIV but moved to 35‰ S after the molt to D (treatment c), or 35‰ S from ZI to J1 (treatment d), lettered treatments corresponding to those in Figure 1. Means with different letters above the error bar differ significantly ($P = 0.05$) within the given experiment for that population with the Tukey-Kramer post hoc test.

animals (92 to 100%) that molted directly from ZIV to D (no ZV) survived metamorphosis to J1, while the percentage that reached J1 among animals which had molted from ZIV to ZV varied from 31 to 83% between treatments (Table 2).

While several larvae of *C. islagrande* also molted to a 5th zoeal stage, the percentage of animals molting directly from ZIV to D (no ZV) was not found to differ significantly between treatments. However, as in the Florida Atlantic population of *C. major*, the presence of ZV did vary between experiments (parental females), and survival to J1 was higher in animals that molted directly from ZIV to D. In both experiments on *C. islagrande*, a few animals molted directly from ZIII to D. A few other larvae were found to be slightly more advanced at the 4th zoeal stage in that they had setae on the pleopods, a character that is usually found at ZV or D (Strasser and Felder, 2000). All of those animals had been maintained at 35‰ S from ZI to ZIII (treatments b, c, d).

Deformed decapodids

While there were several deformed decapodids in both *C. islagrande* and the Florida Atlantic population of *C. major*, only one decapodid from both experiments with the Gulf population of *C. major* was deformed. Deformed individuals most commonly had malformed chelipeds or abdomens. However, some individuals suffered from disfigurements of all limbs. In *C. islagrande*, the percentage of deformed decapodids was low in both experiments (<14%) and did not differ significantly between treatments with Fisher's exact-test (Table 3). Experiment 1 with the Florida Atlantic population of *C. major* was similar to experiments run with the Gulf population in that only one decapodid was deformed. In contrast, the percentage of deformed decapodids was high in both Experiments 2 and 3 with the Florida Atlantic population (Table 3). In Experiment 2, the percentage of deformed decapodids was significantly lower in animals maintained at a constant 25‰ S (treat-

TABLE 2

Percentage of larvae that molted from ZIV to ZV or directly from ZIV to D for populations of *Callichirus* spp. reared under 4 different salinity (‰) protocols (a-d). Numbered experiments are for separate larval clutches. n_0 = number surviving past ZIV; n_1 = number molting from ZIV to ZV; n_2 = number molting from ZIV to D; % n_0 = % surviving past ZIV; % n_1 = % of ZV molting to J1; % n_2 = % of D molting to J1. Percentages of animals that molted from ZIV to D (no ZV) within each experiment, if followed by different letters (x, y, z), differed significantly ($P < 0.01$) according to results of Fisher's exact-test.

Experiments	Molted from ZIV n_0	ZIV to ZV		ZIV to D			
		n_1	% n_0	Reached J1 % n_1	n_2	% n_0	Reached J1 % n_2
<i>Callichirus islagrande</i>							
1 (a) 25‰ ZI to J1	38	9	24	78	29	76 x	83
(b) 35‰ ZI to ZIII, 25‰ at ZIV	37	16	43	75	21	57 x	90
(c) 35‰ ZI to ZIV, 25‰ at D	29	9	31	33	20	69 x	80
(d) 35‰ ZI to J1	30	6	20	50	24	80 x	83
2 (a) 25‰ ZI to J1	39	7	18	71	32	82 x	94
(b) 35‰ ZI to ZIII, 25‰ at ZIV	28	1	4	0	27	96 x	93
(c) 35‰ ZI to ZIV, 25‰ at D	32	0			32	100 x	81
(d) 35‰ ZI to J1	29	0			29	100 x	79
<i>C. major</i> (Gulf of Mexico)							
1 (a) 25‰ ZI to J1	39	0			39	100 x	100
(b) 35‰ ZI to ZIII, 25‰ at ZIV	35	0			35	100 x	97
(c) 35‰ ZI to ZIV, 25‰ at D	40	0			40	100 x	98
(d) 35‰ ZI to J1	37	0			37	100 x	97
2 (a) 25‰ ZI to J1	35	0			35	100 x	97
(b) 35‰ ZI to ZIII, 25‰ at ZIV	39	0			39	100 x	100
(c) 35‰ ZI to ZIV, 25‰ at D	38	0			38	100 x	100
(d) 35‰ ZI to J1	40	0			40	100 x	100
<i>C. major</i> (Florida Atlantic)							
1 (a) 25‰ ZI to J1	39	1	3	0	38	97 x	100
(b) 35‰ ZI to ZIII, 25‰ at ZIV	37	0			37	100 x	97
(c) 35‰ ZI to ZIV, 25‰ at D	39	0			39	100 x	100
(d) 35‰ ZI to J1	39	0			39	100 x	97
2 (a) 25‰ ZI to J1	39	0			39	100 x	97
(b) 35‰ ZI to ZIII, 25‰ at ZIV	39	13	33	69	26	67 y	100
(c) 35‰ ZI to ZIV, 25‰ at D	40	32	80	31	8	20 z	100
(d) 35‰ ZI to J1	40	26	65	69	14	35 z	100
3 (a) 25‰ ZI to J1	40	4	10	50	36	90 x	100
(b) 35‰ ZI to ZIII, 25‰ at ZIV	39	18	46	61	21	54 y	100
(c) 35‰ ZI to ZIV, 25‰ at D	36	23	64	57	13	36 y	92
(d) 35‰ ZI to J1	40	23	58	83	17	42 y	100

TABLE 3

Percentage of decapodids found to be deformed for populations of *Callichirus* spp. reared under 4 different salinity (‰) protocols (a-d). Numbered experiments are for separate larval clutches. n_0 = number of decapodids; n_1 = number deformed among n_0 ; % n_0 = % deformed among n_0 ; % n_1 = % among n_1 (deformed decapodids) that passed through ZV. Percentages of deformed decapodids within each experiment, if followed by different letters (x, y, z), differed significantly ($P < 0.015$) according to results of Fisher's exact-test.

Experiment	(n_0)	Deformed decapodids		
		n_1	% n_0	(with ZV) % n_1
<i>Callichirus islagrande</i>				
1 (a) 25‰ ZI to J1	37	1	3 x	100
(b) 35‰ ZI to ZIII, 25‰ at ZIV	35	2	6 x	50
(c) 35‰ ZI to ZIV, 25‰ at D	29	4	14 x	25
(d) 35‰ ZI to J1	28	0	0 x	
2 (a) 25‰ ZI to J1	30	0	0 x	
(b) 35‰ ZI to ZIII, 25‰ at ZIV	34	1	3 x	0
(c) 35‰ ZI to ZIV, 25‰ at D	34	2	6 x	0
(d) 35‰ ZI to J1	34	4	12 x	0
<i>C. major</i> (Florida Atlantic)				
1 (a) 25‰ ZI to J1	39	1	3 x	100
(b) 35‰ ZI to ZIII, 25‰ at ZIV	37	0	0 x	
(c) 35‰ ZI to ZIV, 25‰ at D	39	0	0 x	
(d) 35‰ ZI to J1	39	0	0 x	
2 (a) 25‰ ZI to J1	39	0	0 x	
(b) 35‰ ZI to ZIII, 25‰ at ZIV	38	9	24 y	100
(c) 35‰ ZI to ZIV, 25‰ at D	38	25	66 z	100
(d) 35‰ ZI to J1	38	23	61 z	100
3 (a) 25‰ ZI to J1	38	1	3 x	100
(b) 35‰ ZI to ZIII, 25‰ at ZIV	35	8	23 y	100
(c) 35‰ ZI to ZIV, 25‰ at D	34	11	32 y	100
(d) 35‰ ZI to J1	40	9	23 y	100

ment a, 0%) than in animals maintained at 35‰ S during the first few stages (treatment b, 24%; treatment c, 66%; treatment d, 61%). Results of Experiment 3 were similar in that animals maintained at 25‰ (treatment a, 3%) had a significantly lower percentage of deformed decapodids than did the other 3 treatments (b, 23%; c, 32%; d, 23%).

DISCUSSION

In the Gulf population of *C. major*, duration of zoeal stages was significantly shorter in animals maintained at 25‰ S than in animals reared at 35‰ S. Decreased S has been shown to accelerate development of other decapod crustaceans (Vinuesa et al. 1985). This effect was also observed when animals were moved from 35 to 25‰ S at

ZIV. The duration of ZIV in animals moved from 35 to 25‰ S at ZIV was similar to that of animals maintained at 25‰ S from hatching. In contrast, the duration of D was not affected by differences in S. This is consistent with previous experiments on this population which demonstrated a decrease in the duration of ZIV with exposure to adult-conditioned water, while the duration of the decapodid stage was unaffected by this stimulus (Strasser and Felder 1998).

As with the Gulf of Mexico population of *C. major*, the duration of the first 3 zoeal stages was shorter in *C. islagrande* when larvae were reared at 25‰ S. However while the duration between molts was longer at 35‰, morphological development was accelerated in some larvae. Several larvae that were maintained at 35‰ S for

the first 3 zoeal stages (treatments b–d) molted directly from ZIII to D, bypassing both ZIV and ZV. Other larvae had setae on the pleopods at ZIV (treatments b–d; 18/96 in Experiment 1, 10/89 in Experiment 2). This is a character that is typically associated with ZV (Strasser and Felder, 2000). None of the larvae reared at 25‰ S molted from ZIII to D or had setae on the pleopods at ZIV.

Unlike in the first 3 zoeal stages, duration of ZIV in *C. islagrande* was longer in animals maintained at 25‰ S than at 35‰ S. However, change in S from 35 to 25‰ at ZIV caused a significant decrease in the duration of this stage. This finding suggests that a change in S may serve as a cue for accelerated development in this species. While both populations of *C. major* were found to accelerate molting from ZIV to D in the presence of sand and adult-conditioned water, *C. islagrande* was unaffected by these stimuli (Strasser and Felder 1998). Duration of D did not differ in animals reared at 35 or 25‰ S. A decrease in S from 35 to 25‰ at ZIV and D also had no effect on the duration of D.

Durations of the first 3 zoeal stages in the Florida Atlantic population of *C. major* were similar at 25 and 35‰ S. Although duration of ZIII was slightly longer in animals maintained at 35‰ S than it was at 25‰ S, the difference was significant only in Experiment 2. The effect of S on the duration of ZIV was not consistent in that there was no significant effect in Experiments 1 and 2, while the duration of ZIV was significantly shorter at 35‰ S in Experiment 3. The effect of S on the duration of D was also inconsistent. While the duration of D was similar between treatments in Experiments 1 and 3, in Experiment 2 duration of D was significantly shorter in animals reared at 25‰ S or moved from 35 to 25‰ at ZIV than in other treatments.

In previous studies, changes in temperature (Knowlton 1965, Ewald 1969, Sandifer 1973, Scotto 1979), amount or type of food (Templeman 1936, Broad 1957), and S (Robertson 1968, Anger 1991) have been shown to alter the number of developmental stages in various decapods. Whereas presence of a 5th zoeal stage did not appear to be related to S in *C. islagrande*, higher S did increase the incidence of ZV in the Florida Atlantic population of *C. major*. In 2 of 3 experiments with larvae of this population, animals reared at 25‰ S usually molted directly from ZIV to D. Animals reared at 35‰ S were more likely to molt from ZIV to ZV. However, transfer at ZIV from 35 to 25‰ S decreased the chances of molting to ZV. Thus larvae passed through fewer instars in lower S water than in higher for this population in which both adults and larvae appear to live typically

in seawater near 35‰ S. *Scyllarus americanus* (Smith) was also shown to alter the number of instars with changes in S, but this species adds stages when reared at lower salinities (Robertson 1968). *Eriocheir sinensis* was shown to add an extra zoeal stage when reared at a lower S; however only 1 of 5 of these larvae successfully molted to D, which subsequently died before metamorphosis (Anger 1991). None of the larvae from experiments with the Gulf of Mexico population of *C. major* passed through a 5th zoeal stage or were deformed at D. Thus larvae from the 2 populations of *C. major* appear to respond differently to S. Other studies have reported variability in the number of instars between different populations of the same caridean shrimp species (Ewald 1969, Sandifer 1973).

A large percentage of the decapodids were deformed in Experiments 2 and 3 with the Florida Atlantic population of *C. major*. More decapodids were deformed in treatments maintained at 35‰ from ZI to ZIII (treatments b–d) than when maintained at 25‰ S at these stages. The higher incidence of deformity in these treatments appears related to the addition of a larval instar, as all deformed decapodids had passed through a 5th zoeal stage. In previous experiments with this population of *C. major*, the presence of sand and adult-conditioned water at ZIV triggered most animals to molt directly from ZIV to D (no ZV), which led to few deformed decapodids (Strasser and Felder 1999b). In *C. islagrande* the incidence of deformity was low and did not differ significantly among treatments. Unlike the case with Florida Atlantic *C. major*, deformed decapodids were not necessarily restricted to individuals that passed through ZV. Higher salinities also led to deformed decapodids in a population of *Rhithropanopeus harrisi* (Gould) from Portugal (Gonçlaves et al. 1995) and another from North Carolina (Christiansen and Costlow 1975).

Decapodids of *C. sapidus* have been shown to accelerate molting to J1 with a decrease in S at this stage (Forward et al. 1994). Neither *C. major* nor *C. islagrande* accelerated molting from D to J1 in response to a decrease in S, which suggests that decapodids are not responding to decreased S as a cue for settlement. Both *C. islagrande* and the Gulf population of *C. major* accelerated the zoeal phase of development at lower salinities which may contribute to larvae of these animals being retained in nearshore waters. ZIV larvae of both species have been collected in waters near the adult habitat in Louisiana. In general, response of larvae to different salinities was more similar between the Gulf of Mexico populations of 2 different species, than it was between Gulf and Atlantic populations of *C. major*. Thus the adult

habitat seemed to predict the response of larvae to S to a greater extent than did phylogenetic proximity.

ACKNOWLEDGEMENTS

We thank B.E. Hasek, J.G. MaKinster, R.B. Manning, S.F. Nates, and K.M. Strasser who assisted with field collections and provided other assistance, and M.E. Rice, Director of the Smithsonian Marine Station-Fort Pierce, FL, who facilitated access to station facilities used during analytical phases of this project. We also thank R.T. Bauer, R.G. Jaeger, R. Lemaitre, and G.M. Watson for their comments on the manuscript. Direct support for this study was provided by a doctoral fellowship from The University of Louisiana-Lafayette, a graduate student research grant from the LUMCON (Louisiana Universities Marine Consortium) Foundation, and a summer research award from the Smithsonian Marine Station to Karen M. Strasser. Additional support for field and lab activities was provided to D.L. Felder under Louisiana Sea Grant College Program Grant R/CFB-21, US Fish and Wildlife Service Cooperative Agreement 14-16-0009-89-96 (Task Order No. 6), US Department of Energy grant DE-FG02-97ER12220, and several small project grants from the Smithsonian Marine Station. Views expressed herein are those of the authors, and do not necessarily reflect views of supporting government agencies or subagencies mentioned above. This is contribution No. 505 for the Smithsonian Marine Station and contribution No. 68 for the ULL Laboratory for Crustacean Research.

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